PROC. ENTOMOL. SOC. WASH.
92(4), 1990, pp. 778–792

REDESCRIPTION AND IMMATURE STAGES OF *FICIOMYIA PERARTICULATA* (DIPTERA: CECIDOMYIIDAE), A GALL MIDGE INHABITING SYCONIA OF *FICUS CITRIFOLIA*

J. C. Roskam and H. Nadel

(JCR) University of Leiden, Dept. of Population Biology, Schelpenkade 14a, 2313 ZT Leiden, Netherlands; (HN) University of Florida, Tropical Research and Education Center, 18905 S. W. 280th Street, Homestead, FL 33031.

Abstract.—Felt described *Ficiomyia perarticulata* and *F. birdi* from syconia of *Ficus aurea* Nutt. and *F. citrifolia* Mill., respectively, collected in southern Florida. We put *Ficiomyia birdi* Felt into synonymy because qualitative, quantitative and principal component analyses revealed no differences between Felt's type series of *F. perarticulata* and *F. birdi*. Felt's host plant record for *F. perarticulata* is probably wrong. After extensive sampling we conclude that the host-plant association of *Ficiomyia*, at least in Florida, is restricted to *Ficus citrifolia*. We redescribe the adult stages of *Ficiomyia perarticulata* and describe the immature stages for the first time. Adult males have considerably fewer antennal segments than females, which is otherwise unknown in gall midges. Other peculiarities include the development of a spatula in the second larval instar and the development of sexually dimorphic galls. Females cause longer, stalked galls and males sessile galls.

Key Words: *Ficiomyia, Ficus,* gall midge, immature stage, sexual dimorphism, emergence, principal component analysis (PCA), host-plant association, biogeography

One of the most striking examples of mutualism among phytophagous insects and their host plants is the association between figs and agaonid fig wasps. This association resulted in patterns of radiation that display remarkable co-evolved traits between the insects and figs. Fig wasps, which pollinate fig flowers and, in turn, use ovaries as larval development sites, are not the only group of insects that inhabit fig fruit. Other Hymenoptera, as well as gall midges, inhabit syconial galls (Docters van Leeuwen-Reijnvaan and Docters van Leeuwen 1926, Williams 1928, Barnes 1948, Condit 1969, Mani 1973). Felt (1922, 1934) erected the genus *Ficiomyia* for midges inducing pocket-like swellings within syconia of figs native to Florida, and described two species, *F. perarticulata* on *Ficus aurea* Nutt. and *F. birdi* on *Ficus citrifolia* Mill. (= *F. laevigata* Vahl). Both species are characterized by a large number of antennal segments, a reduced number of palpal segments, and peculiar male genitalia. Felt (1925) placed *Ficiomyia* in the tribe Dasyneuriariae: Gagné, in McAlpine et al. (1981) placed it, and all other Dasyneuriariae, in the tribe Oligotrophini. Like *Ficus, Ficiomyia* may extend into Florida from the Neotropics. Close relatives of the midge are unknown.

Because Felt described both species from a few poor and incomplete specimens, he drew some erroneous conclusions concerning species differences and probably reported an incorrect host plant association. These errors became apparent after we analysed Felt's type series and a large sample of fresh specimens reared from authoritatively identified host plants. In this paper we redescribe *F. perarticulata* Felt and place *F. birdi* into synonymy. Extensive sampling of the purported host plant species native to Florida, and a comparison of both of Felt's type series with the midges we reared, show that his material, attributed to two species, is conspecific. We also described the immature stages of *Ficiomyia*, which, like the adults, possess some remarkable traits. Lastly, we described some aspects of the midge's biology, including emergence behavior and periodicity, mating, and the sex ratio.

METHODS

We studied newly reared material and compared it with Felt's type series. Samples of syconia in various stages of development were dissected to determine the presence and abundance of midge galls. Immature stages were macerated in warm 80% lactic acid. First instar larvae were mounted in polyvinyl-lactophenol. Larvae of later instars and pupae were mounted in Euparal. Fruits of identified fig species were isolated in vials to rear adult gall midges. Adults were stored in 70% alcohol and eventually mounted in Euparal using the method outlined in Roskam (1977). Adult terminology follows McAlpine et al. (1981); for larval terminology, see Möhn (1955), and for pupal terminology Möhn (1961). All measurements were taken from slide-mounted material. The statistical methods are explained in the paragraph dealing with the comparison of new material with Felt's type series.

Behavioral observations were made in several locations in Dade and Monroe Counties, Florida. Sex ratio and periodicity of midge emergence from galls were studied in excised fruits which were isolated in plastic vials with mesh caps and ambient conditions.

Ficiomyia perarticulata Felt

Ficiomyia perarticulata Felt 1922: 5.
Ficiomyia birdi Felt 1934: 132. New Synonym.

For quantitative characters, see Tables 1 and 2.

Male.—*Head:* Eyes very large, holoptic, about 11 facets long at vertex; facets hexagonal, closely abutting one another (Fig. 1). Occiput diamond-shaped, largely covered with setae (Fig. 2). Antenna with 29–31 stalked flagellomeres, the fused first and second flagellomeres counted separately; node with a basal whorl of short, rigid setae and long, bent setae on horseshoe-shaped sockets scattered over its anterosubdistal surface, circumfila appressed, forming one complete basal whorl and a partial, anterodistally situated whorl, the two connected at the medial and lateral surfaces of the node (Fig. 6). Antennal plate and clypeus covered with many setae; labrum sclerotized; labium heart-shaped; labella hemispherical in lateral view, the distal half covered with rigid setae. Palpus 3-segmented, basal segment partly to completely fused with second, third segment variable in length; basal segment with two to six laterally-situated, long setae (Fig. 3).

Thorax: Scutum with four longitudinal rows of setae interspersed with scales. Scutellum with scattered setae and scales. Anepisternum with three groups of anterodorsally, anteroventrally and centrally situated setae and scales. Anepimeron with a central group of setae and scales. Legs densely covered with scales; claws toothed, teeth usually bifid, first tarsomere of all legs with pointed asetulose lateroventral projection (Fig. 5); empodia as long as or slightly longer than claws and twice as long as pulvilli (Fig. 4). Wing densely covered with scales, hyaline if scales absent, maculate if scales pres-

Table 1. Quantitative comparison of newly collected material with Felt's type series, males. All measurements are in μm, bold-printed values indicate ranges for Felt's series which exceed the ranges of the newly collected material. *, characters used for PCA.

	perarticulata new				*birdi* Felt		*perart.* Felt	
Character	N	Mean	cv %	Range	N	Range	N	Range
*he head	11	584	1.7	568–598	3	568–**637**	1	**617**
he antennal plate	11	198	3.6	184–208	3	**162**–184	1	184
nr flagellomeres	8	30	2.8	29–31	1	30	0	—
le antenna	8	2879	5.0	2684–3063	1	2716	0	—
*le 10 flagellomeres	11	1011	3.3	947–1074	2	917–1074	2	995–1074
le node 5. flagm.	11	68	7.0	63–77	2	68–70	2	63–75
wi node 5. flagm.	11	60	3.3	56–63	2	58–61	2	56–61
le stalk 5. flagm.	11	38	9.3	31–41	2	39–39	2	41–41
le seta node 5. fm.	8	255	10.0	223–300	3	290–**339**	2	227–**307**
le 3. palp segment	8	39	16.3	29–46	0	—	0	—
*le metafemur	11	1473	3.0	1421–1547	1	1532	2	1437–1468
le metatibia	11	1438	5.7	1295–1547	1	1437	2	1421–1500
le 2. metatarsus	11	1172	3.2	1105–1232	1	1232	2	1137–1263
le 5. metatarsus	11	229	4.8	205–237	0	—	1	221
wi wing	11	1061	3.6	979–1103	3	1074–**1232**	1	**884**
le vein R1	11	939	4.4	884–995	3	**1026–1184**	1	**1105**
*le vein R5	11	2367	2.6	2290–2495	3	**2605–2842**	1	2416
le basal branch Cu	11	687	4.9	647–742	3	647–**774**	0	—
le proximal br. Cu	11	1451	3.4	1374–1547	3	1515–**1768**	0	—
le distal br. Cu	11	812	4.8	758–900	3	**979–1011**	0	—
le gonocoxite	11	242	3.5	227–254	2	247–252	2	237–249
le lobe gonocoxite	11	128	7.5	104–138	2	116–121	0	—
wi gonocoxite	11	81	10.3	68–92	2	68–73	0	—
*le gonostylus	11	111	1.8	109–114	2	**99–121**	1	**116**
incisision cercus	11	96	12.9	80–121	2	97–102	2	92–94
incis hypopr	11	90	12.1	70–106	2	77–80	2	85–90

ent (fresh material) due to patches of broad, pigmented scales among patches of narrow, hyaline ones; R5 almost straight, declining at the very end towards wing tip and terminating slightly anterior to it, Cu forked, its branches straight (Fig. 8).

Abdomen: oblong cylindrical, yellowish and densely covered with broad, dark brown scales. Tergites 2–6 rectangular, with simple, uninterrupted, posterior rows of setae, lateral setae lacking, two trichoid sensilla on anterior margins, sclerotized parts covered with scales, tergite 4 about 2.5 times as wide as long, tergite 7 narrower, with double row of posterior setae, tergite 8 not sclerotized, indicated by some posterolaterally situated setae, trichoid sensilla present; pleura thickly covered with scales; sternites 2–7 rectangular, wider than long, setae in double rows on posterior margins, scattered along lateral margins and on anterolateral parts, a pair of closely placed trichoid sensilla on medioanterior margin, sclerotized parts with scattered scales, sclerite 8 narrower and without trichoid sensilla. Cerci rounded posteriorly, with rigid setae on posterior parts of both surfaces, arrangement of microtrichia in transverse, elongate patches anterodorsally, gradually changing to a scattered arrangement posteriorly, ventral surface with microtrichia in transverse rows; hypoproct variable, oblong, parallel-sided, and deeply emarginate, with microtrichia scattered on its dorsal surface and in transverse rows on the ventral surface, each lobe with two to three apical setae; gonocoxite oblong, narrowed at mid length, with a conspicuous apicoventral lobe, setae mainly on

Table 2. Quantitative comparison of newly collected material with Felt's type series, females. For further explanation, see Table 1.

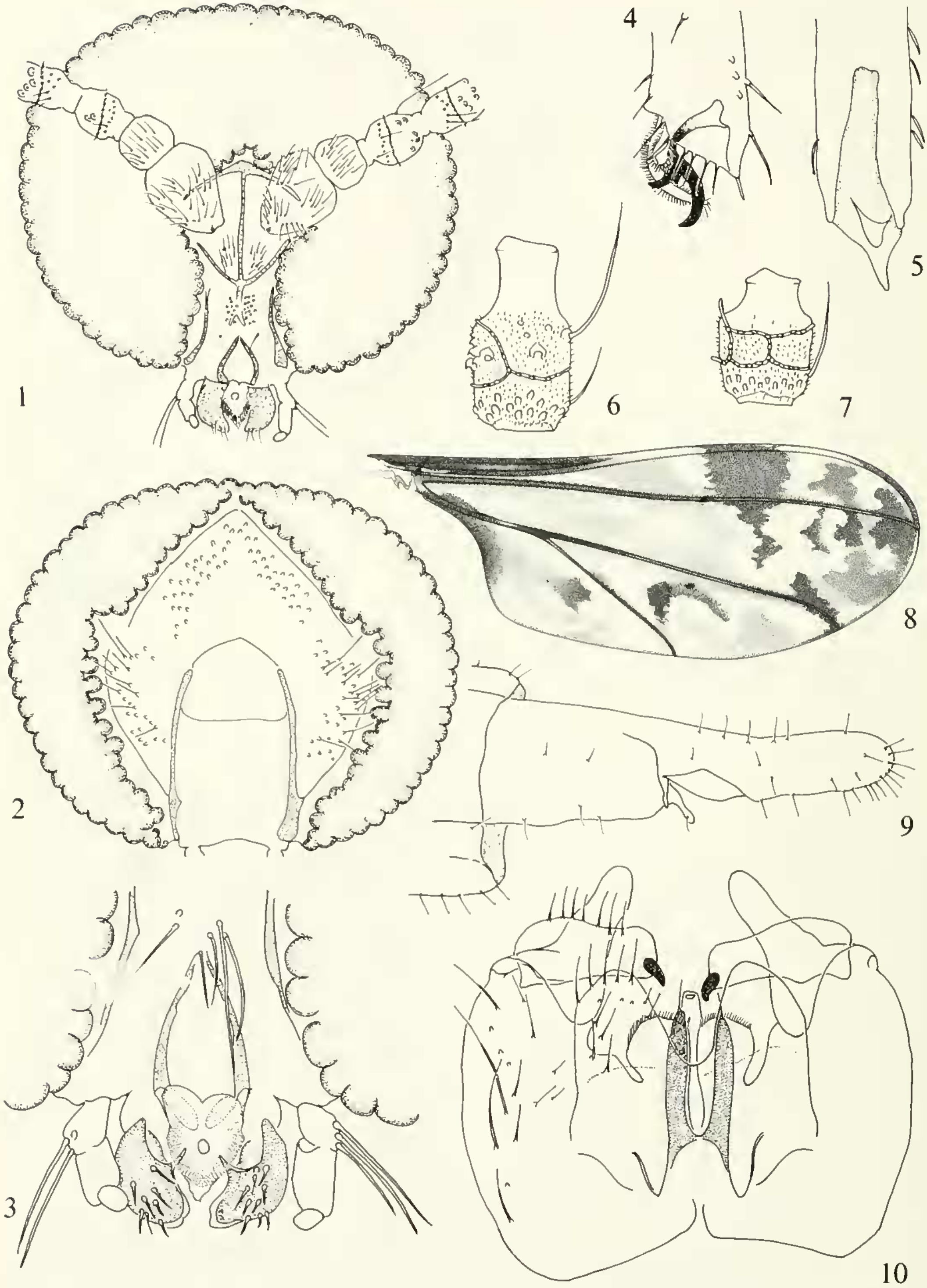
Character	*perarticulata* new				*birdi* Felt		*perart.* Felt	
	N	Mean	cv %	Range	N	Range	N	Range
*he head	11	584	3.0	559–608	2	**549–568**	4	568–608
he antennal plate	10	193	6.5	184–201	1	169	3	186–**203**
nr flagellomeres	9	38	2.2	37–39	0	—	2	39–39
le antenna	9	2482	5.8	2290–2700	0	—	1	**2921**
*le 10 flagellomeres	11	723	4.1	679–774	1	**790**	1	**821**
le node 5. flagm.	11	56	5.7	51–63	1	58	1	53
wi node 5. flagm.	11	57	4.8	53–61	1	58	1	**63**
le stalk 5. flagm.	11	23	10.9	19–24	1	**27**	1	24
le seta node 5. fm.	11	106	21.2	82–145	1	**148**	1	85
le 3. palp segment	10	41	27.0	24–58	0	—	1	34
*le metafemur	11	1503	5.4	1405–1642	2	1547–1579	3	1579–**1705**
le metatibia	11	1457	6.9	1342–1611	2	1547–1705	3	1611–**1721**
le 2. metatarsus	8	1153	8.4	963–1263	1	**1421**	0	—
le 5. metatarsus	7	229	5.0	221–237	0	—	0	—
wi wing	11	1192	3.8	1137–1263	2	1326–1405	2	1168–1326
le vein R1	11	1041	4.1	995–1105	2	1137–1231	2	1137–1200
*le vein R5	11	2626	3.7	2526–2779	2	**3047-3363**	2	2684–**3174**
le basal branch Cu	11	748	5.3	695–821	1	**916**	2	**679-868**
le proximal br. Cu	11	1652	4.9	1547–1753	2	**2053-2116**	2	1721–**2100**
le distal br. Cu	11	895	4.3	837–947	2	1105–1105	2	**995-1058**
le cercus	10	177	4.7	165–189	0	—	2	**143**–155
*he cercus	11	49	6.3	44–53	1	51	3	44–48
le hypoproct	11	28	17.1	22–34	1	29	3	29–39

distal part of dorsal surface and scattered over lateral and ventral surfaces; gonostylus cylindrical, blunt at apex, with curved, stout, apical tooth and with numerous setae, mainly on its lateral surfaces; mediobasal lobe about half as long as gonocercus, stout, blunt, with transverse, narrowly oblong patches of microtrichia; aedeagus slender, parallel sided, and distinctly longer than the mediobasal lobes (Fig. 10).

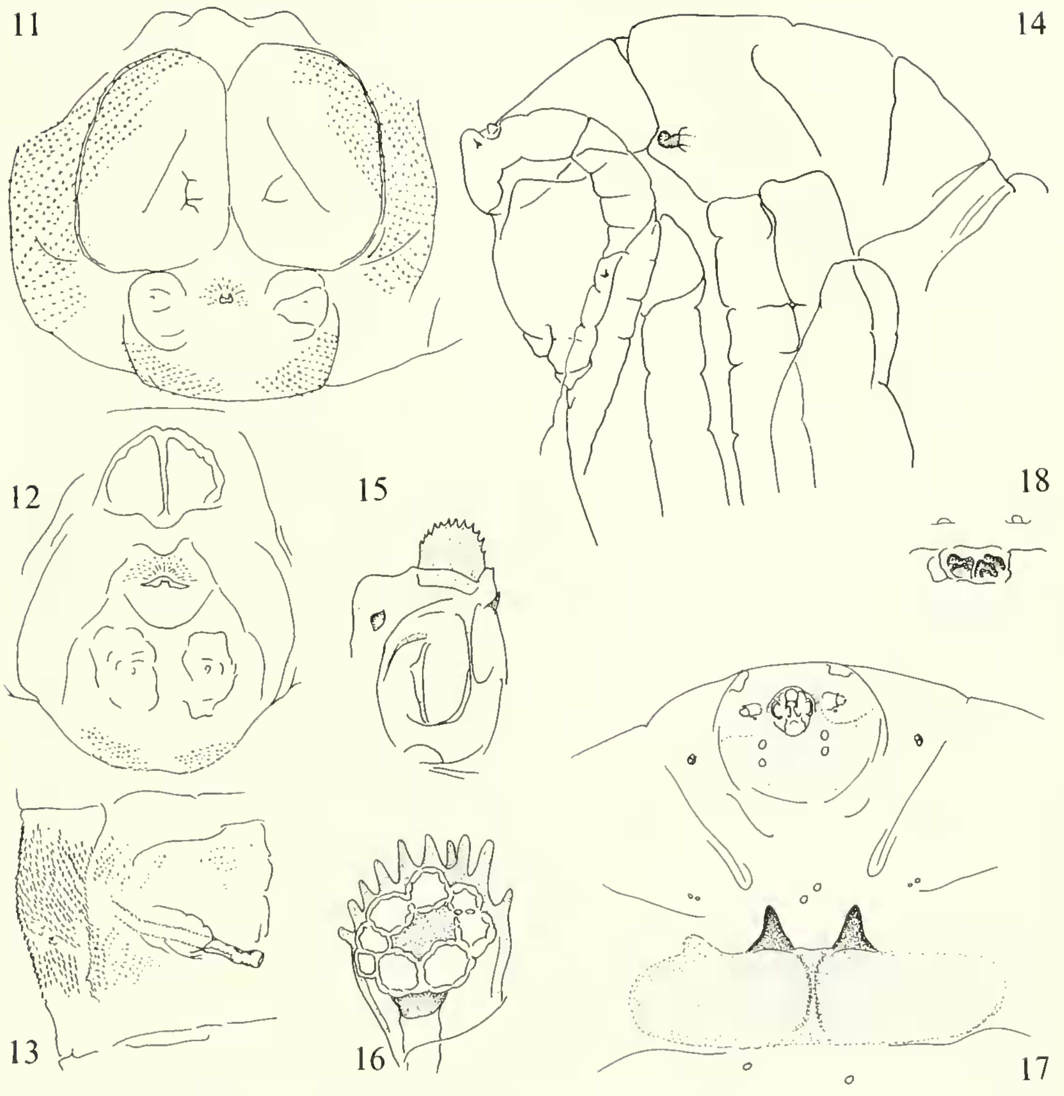
Female (characters not mentioned similar to those of the male).—*Head:* Antenna with 37–39 stalked flagellomeres; node with only basal whorl of short setae and complete, laterally and medially interconnected circumfila (Fig. 7).

Abdomen: ovoid, deep orange-red; spermathecae conspicuously pigmented. Ovipositor telescoped, abdominal segment 9 about 1.5 times as long as segment 8, with setae scattered all over its surface, the microtrichia in groups, forming a reticulate pattern, one pair of trichoid sensilla on anterolateral margin; segment 10 slightly longer than segment 9, with microtrichia in dense transverse rows; cercus oblong, with setae scattered over whole surface, the longer ones mainly distal, microtrichia densely scattered anteriorly, in more or less reticulate pattern posteriorly; hypoproct short, obtuse-triangular, with microtrichia in transverse rows (Fig. 9).

Pupa.—Color turning from creamy-white to yellowish in male and pink-orange in female. Apical and lateral spines on head, as well as lateral facial papillae, which are usually present in gall midge pupae, absent and indicated by blunt projections. One pair of trichoid sensilla on apical projections (Fig. 14). Thoracic horns absent, prothoracic spiracle protruding from its respective surface. Abdomen with five pairs of protruding spiracles, on segments 2–6, the pair of stigmata on segment 7 vestigial (Fig. 13). On seg-



Figs. 1–10. *F. perarticulata*, adult structures. 1, Male head, frontal. 2, Same, distal. 3, Mouthparts. 4, Detail of male hind fifth tarsomere. 5, Detail of distal part of male hind first tarsomere. 6, Male fifth flagellomere. 7, Female, same. 8, Male wing. 9, Ovipositor. 10, Male postabdomen, dorsal. 8, ×25. 1–2, ×100. 9–10, ×180. 6–7, ×240. 4–5, ×290.



Figs. 11–18. *F. perarticulata*, structures of immature stages. 11, Male pupa, distal view of ultimate abdominal segments. 12, Female pupa, same. 13, Male pupa, stigma and skin structures on sixth abdominal segment, lateroventral. 14, Male pupa, head and thorax, lateral. 15, Third instar larva, antenna. 16, Same, stigma on first thoracic segment. 17, Same, head, supernumerary segment and first thoracic segment with spatula, ventral. 18, Second instar larva, detail of spatula. 14, ×65. 13, ×100. 11–12, 17, ×150. 18, ×450. 16, ×725. 15, ×1450.

ments 2–6, three pairs of dorsal trichoid sensilla and one pair of pleural sensilla, the sublateral pair of dorsals closely situated to the intermediate pair. On segment 7, one pair of dorsals and one pair of laterals. Dorsal and lateral surfaces with pointed setulae, ventral surface glabrous. Male pupa with two large posterior convexities in which the gonocoxites develop; female pupae with these cavities vestigial (Figs. 11–12).

Third (final) instar.—Body obconic, with broad thorax and upwardly curved, gradually narrowing abdomen, creamy-white; segmentation as usual for gall midge larvae and consisting of head (h), supernumerary segment (ss), three thoracic (t1–3), nine ab-

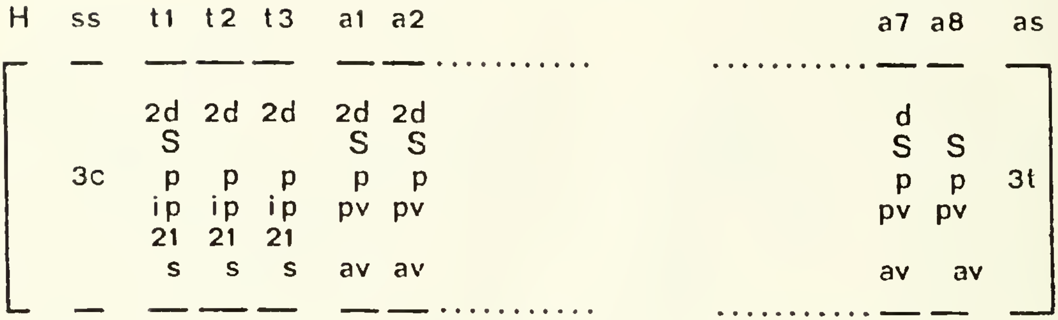


Fig. 19. *F. perarticulata,* diagram of pattern of papillae and tracheal system of third instar larva. a1–8, abdominal segments. as, anal segment. av, anterior ventral papilla. c, collar papilla. d, dorsal papilla. h, head. ip, interior pleural papilla. l, lateral papilla. p, pleural papilla. pv, posterior ventral papilla. S, stigma. s, sternal papilla. ss, supernumerary segment. t, terminal papilla. t1–3, thoracic segments.

dominal (a1–9), of which the final one is the anal segment (as). Body length 1850–2520 μm, width 850–1410 μm, head capsule width 123–157 μm, width between antennae 53–70 μm. Head capsule flat, weakly sclerotized, antennae truncate with sclerotized, plumose appendages (Fig. 15); thoracic surface glabrous, anteroventral surface of a2–a7 with about 25 transverse spinule-rows, a8 with such rows on its posteroventral surface. Spatula transverse, bilobed, the lobes acute; stalk not differentiated. Spatula height 94–126 μm, width 236–314 μm, height of lobes 34–46 μm, distance between tips 48–85 μm (Fig. 17). Respiration peripneustic, with spiracles on t1 and a1–a8; spiracles with oblong sclerotized outgrowths (Fig. 16). Papillae, unless indicated otherwise, without setae; pattern of papillae; three pairs of lateral collar papillae, the papillae of two of these pairs abutting (Fig. 17); thoracic segments with one pair of sternal papillae each, the pair on t1 abutting and confined by the spatula lobes (Fig. 17), two pairs of abutting laterals with short setae, one pair of interior pleurals, two pairs of dorsals; segments a1–a7 with one pair of anterior ventral papillae, one pair of posterior ventrals, one pair of laterals and two pairs of dorsals; a8 with dorsal papillae missing; anal segment with usually three pairs of terminal papillae, anal papillae absent (Fig. 19). N = 10.

First instar.—Body ellipsoid, transparent. Body length 588–735 μm, width 225–254 μm. Head capsule width 33–41 μm, flattened, with truncate antennae. Body surface glabrous with patches of minute spinule-rows on dorsal and ventral surfaces. Spatula absent. Respiration apneustic with a pair of vestigial spiracles on abdominal segment 8. All papillae without setae except the pleural pair on abdominal segment 8. Pattern of papillae basically as in third instar; the pair of pleural papillae on abdominal segment 8 very distinct and with short setae. N = 4.

Second instar.—Body ellipsoid, creamy-white. Body length and width not defined because of the poor condition of the material. Head capsule width 87 μm, head capsule convex, with truncate antennae. Body surfaces as in first instar. Spatula present, bilobed, stalk not differentiated, width 17 μm, between lobes 7 μm (Fig. 18). Respiration peripneustic, with spiracles situated as in third instar, width of first thoracic spiracle 10 μm. Pattern of papillae as in third instar. N = 1.

Gall.—Barnes (1948) described the gall as an enlarged seed capsule which becomes abnormally lengthened. However, because the young gall may bear one to three flowers on its exterior, the gall must be considered a pocket-shaped outgrowth of the receptacle (Fig. 20). The associated flowers are gradually reduced as the gall matures. One larva is present per gall. The first instar is oriented with its head towards the syconial cavity and is completely enclosed by the gall tissue; the head is traceable by a pair of dark eyespots (Fig. 21). A gall chamber becomes distinct when the larval spatula develops. At the late pupal stage a conspicuous 'crown,' with a central window-pit, grows from the top of the gall on the fruit surface. Often, two or three galls are concentrated around one window-pit. One to several crowns occur per galled fruit.

Two shapes are distinguished in mature galls (Fig. 22): shorter, sessile galls with the gall chamber situated close to the window-pit, and longer, stalked galls with a distinct constriction between gall chamber and window-pit. Males developed exclusively in the sessile galls, and females in the stalked galls. This was determined by dissection of pupae from galls (N = 15 per gall type), and dissection of galls after emergence of adults (N = 30 per gall type). Such a dimorphism has also been reported by Coutin and Riom (1967) for *Mikiola faqi* Hartig on beech in Europe.

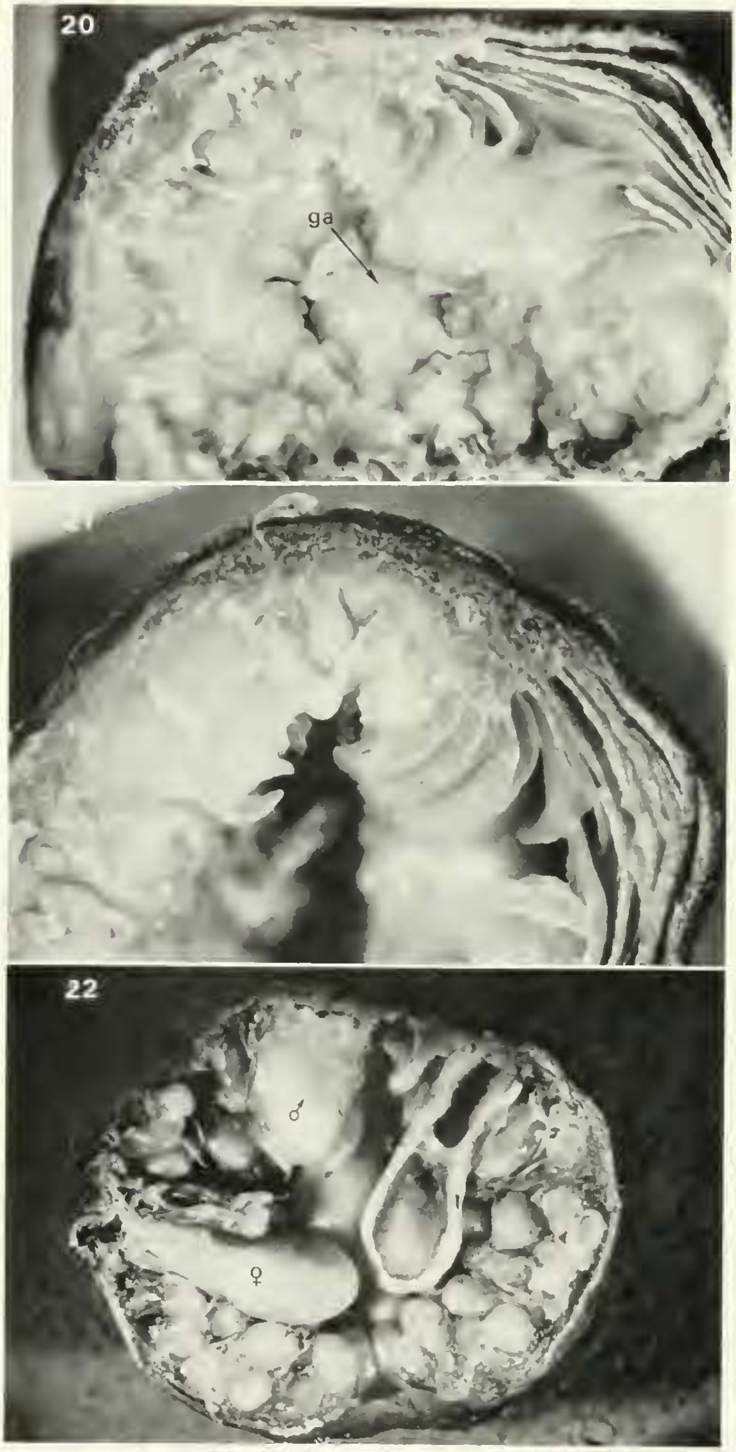
Types.—Felt did not designate holotypes from among his type series. Lectotypes are therefore designated here by one of us (JCR). For *F. perarticulata* slide "a," male, with left hand label "Lectotype, design. by J. C. Roskam 1989"; for *F. birdi* the slide marked with "type" by Felt, male, remounted by R. J. Gagné, again with left hand label "Lectotype, design. by J. C. Roskam 1989." All specimens of both Felt series belong to the New York State Museum at Albany and are now on indefinite loan to the Systematic Entomology Laboratory in Washington, D.C. The specimens we mounted have been deposited in U.S. National Museum in Washington.

COMPARISON OF NEW MATERIAL WITH FELT'S TYPE SERIES

The type series of *F. perarticulata* consists of 10 slides with specimens or fragments mounted in Canada balsam. Felt (1922) described the specimens as "somewhat broken in transit and as a consequence, the descriptions . . . are not complete in certain details." All slides are labeled "Ficiomyia perarticulata Felt on Ficus aurea Miami, Fla. Feb. 9 '22 Type a32128." On two of these slides, labeled by one of us (JCR) with "male a" and "male b," a male is mounted, both with incomplete antennae and shriveled heads and legs. Five slides, labeled with "female a"–"female e," bear incomplete females. All this material was cleared before mounting. A slide labeled "f" contains two wings of different sizes, apparently taken from specimens before clearing; a slide labeled "g" contains a complete female flagellum in shriveled condition. Finally, a slide marked "h" contains a mixture of incomplete male and female flagella, legs, and the thorax and gaster of a female fig wasp, *Pegoscapus* sp. (species identification not possible without the head). The type series of *F. birdi* Felt consists of three slides with a male on each and two slides with a female on each. One male and one female are marked "type"; all slides are labeled "Ficiomyia birdi Felt Florida 1933." The male that we designate as lectotype has been cleared and remounted by R. J. Gagné, Washington, D.C. (R. J. Gagné, in litt.). Felt's (1934) statement about the number of antennal segments is based on material of the male marked "b" by JCR. All material, specimen "b" excepted, has incomplete antennae and legs and shriveled palpi.

The lobed gonocoxites and the high number of stalked antennal segments in both sexes, characters on which the genus *Ficiomyia* was erected, are distinct in the material of both type series. The statements "palpi probably uniarticulate" (Felt 1922) or "palp consisting of one, slender, rather long segment" (Felt 1934), which are used to distinguish *Ficiomyia* (Felt 1925, Gagné in McAlpine et al. 1981) are not correct. These must be replaced by "palpi usually 3-segmented, with the first and second segments partly to completely fused."

Examination of new material revealed that



Figs. 20–22. Longitudinal sections of infested *F. citrifolia* syconia. 20, Gall with reduced flowers on its exterior (ga). 21, Gall with first instar gall midge larva. 22, Syconium with two stalked (female) and one sessile (male) gall. 22, ×8. 20–21, ×12.

the species differences presented by Felt (1934) for *F. perarticulata* and *F. birdi* are not valid. The difference in body color is apparently due to different clearing of the material. The fuscous markings on the wings reported by Felt (1934) of *F. birdi* (caused by a thick layer of scales) are absent in the material of *F. perarticulata*, but this is probably an artifact: the scales are easily dislodged in alcohol-stored material. The most striking difference reported by Felt, however, concerns the number of antennal segments. He apparently used a complete female antenna for his description of *F. perarticulata*, whereas he used the antenna of a male in his description of *F. birdi*. This difference in the number of antennal segments, though, is not due to a species difference but to sexual dimorphism. This is the first record of considerably fewer flagellomeres in males than females in Cecidomyiidae. Male cecidomyiids generally have as many or a few more flagellomeres than females. *Ficiomyia* is, therefore, remarkable among gall midges (for a review, see Mamaev 1968). Finally, we doubt the identification of the host plant of *F. perarticulata*. For a discussion, see the section on host plant associations.

Because we found no qualitative characters to differentiate between the two species, we sought differences by using quantitative analysis. The quantitative traits are listed in Tables 1–2. Although both of Felt's series comprise considerably less material than the material we reared, his material is more variable. His midges are generally larger, but in eight cases from both series some characters exceeded both the lower and upper boundaries of the ranges set by our material. Therefore, although our material should be conspecific with one of Felt's series, the difference between the Felt material and our midges is larger than the difference between Felt's series. Based on this analysis, we again find no evidence to support the view that *F. perarticulata* and *F. birdi* are different species.

With principal component analysis (PCA) it is possible to analyse several characters simultaneously; the technique therefore allows a more accurate judgment on the status of *F. perarticulata* and *F. birdi*. For a description of the technique and an outline of its possibilities, see Pimentel (1979). Among its attributes, PCA results in a graphic representation of specimens in a coordinate system with axes that show zero intercorrelations and to which the original characters (by measured values of the data matrix) have contributed proportionally to their variation. Put otherwise, the original axes, representing the characters, are rotated while the original relationships among the data points, representing the specimens, are maintained.

If *F. perarticulata* and *F. birdi* are different species, they should take different positions in a PCA hyperspace. The members of one of such supposed species should occupy closer mutual positions than members of a different species. The data matrix consists of values measured for the specimens we reared. Because the technique does not allow missing values, and missing values are frequent in Felt's type series, we represented the type series by mean values (Tables 1, 2). We are aware of the flaws of this decision but, given the poor condition of the material, it was our best option. Therefore, apart from the matrix of 11 specimens per sex we include two 'type representatives,' one for *F. perarticulata* and one for *F. birdi*, again per sex.

The data matrix is standardized (means zero, standard deviations 1) because the characters used are of a different size order (Tables 1, 2). The values for Felt's material have been standardized using the mean values and standard deviations from the characters as listed in Tables 1 and 2. All characters were tested for normality. A PCA technique constrains the number of characters which can be used relative to the number of specimens, and, in our case necessitates a low 'within species variation.'

We therefore chose a limited number (5) of characters showing a low coefficient of variation (Tables 1, 2). We selected these characters from different body regions to avoid combinations of characters with high intercorrelations (e.g. different parts of one leg). The PCA was done for males and females separately.

Results.—Males (Fig. 23). The type series of *F. perarticulata* (P) and *F. birdi* (B) are excentrally situated: both represent large midges. The *F. perarticulata* representation (P) is nearest to the centroid, even closer than specimen marked i. The latter specimen, like all others (a–k), supposedly belongs to *F. birdi* on the basis of host plant association. The *F. birdi* representation (B) is situated farthest from the centroid, but, on the other hand, is so closely situated to specimen i that we cannot assign it to a separate species. For females (Fig. 23) the result is even clearer: here both *F. birdi* and *F. perarticulata* representations are excentric, but mutually very close. Therefore we must conclude again that *all* material, i.e., Felt's type series *and* our material, is conspecific, and *F. birdi* must be put into synonymy for reason of priority.

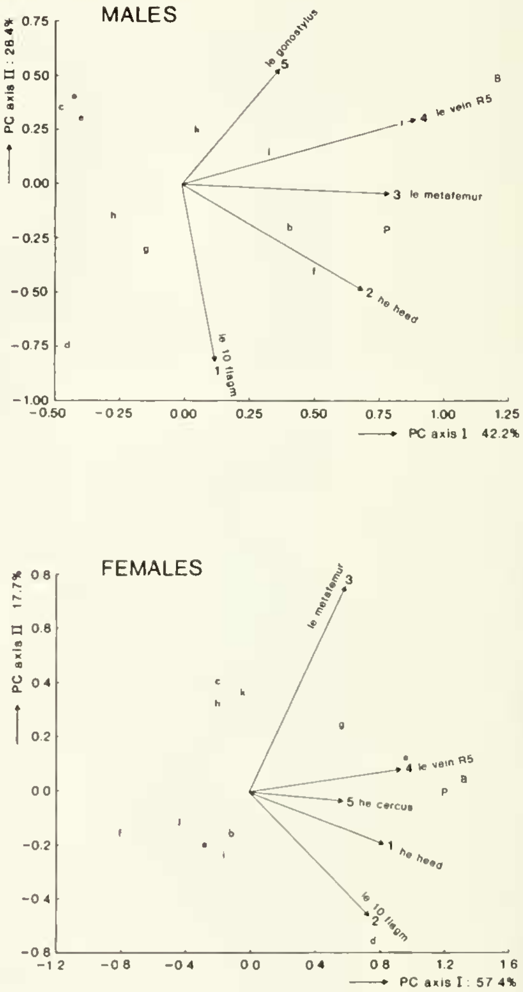


Fig. 23. Principal component analysis of adult characters. The vectors indicate amount and direction in which the separate characters attribute to the position of the specimens. a–k, Newly reared specimens. B, Representation of *F. birdi.* P, Same, *F. perarcticulata.* For further explanation, see text.

Distribution and Host Plant Association

Ficus aurea, the Florida strangler fig, and *F. citrifolia,* the shortleaf fig, are native to Florida. The Florida strangler fig is more abundant and occurs also on the Bahama Islands. The shortleaf fig is restricted in Florida to hammocks in the southernmost part and the Florida Keys, and occurs also in the Bahamas and the West Indies (Elias 1987). Although we examined many samples of *F. aurea,* we never found *Ficiomyia* or its parasitoid, *Physothorax bidentulus* Burks, in this fig species (there is one record of *P. bidentulus* from *F. aurea,* in Burks (1969), but it is from the same collection from which *F. perarticulata* was described). D. McKey, botanist at the University of Florida at Miami has also never found the conspicuous *Ficiomyia* galls in syconia of *F. aurea* (pers. comm.). The record of *Ficiomyia* on *F. aurea,* therefore, was probably due to a misidentification of the host plant. The host plant of *F. perarticulata* has also been erroneously listed as *F. carica* in Gagné (1989).

We examined the following samples: *Ficus aurea,* Dade Co., Miami, 3-22-89, leg. H. Nadel and J. C. Roskam, 147 syconia, diameter 5–8 mm, two kinds of ovaries, small and large, containing different species of fig wasps, the species in the larger ovaries containing *Physothorax;* Dade Co., Miami, 3-22-89, leg. H. Nadel and J. C. Roskam, 50 syconia, diameter 5–8 mm, two sizes of fig wasp-containing ovaries, the larger containing *Physothorax;* Dade Co., Miami, 3-22-89, leg. H. Nadel and J. C. Roskam, 50 syconia, diameter 5–6 mm, ovipositing agaonids, no size differences among ovaries; Lee Co., Sanibel Island, 3-25-89, leg. H. Nadel and J. C. Roskam, 100 syconia, diameter 5–9 mm, small and large ovaries, one *Physothorax russelli* Crawford. Monroe Co., No Name Key, 9-17-88, leg. H. Nadel, 15 syconia, diameter 7–8 mm, some with many fig wasps, no midge galls. Monroe Co., Key Largo, 9-12-88, leg. H. Nadel, 46 syconia, diameter 5–8 mm, some with remnants of founding fig wasp females, others with almost emerged fig wasps, no midge galls.

Ficus citrifolia, Dade Co., Miami, 6-24-88, leg. H. Nadel and M. Matthews, 49 syconia, diameter 7–10 mm, with fig wasp remnants; 31 syconia with 80 galls, second and third instar midge larvae, midge pupae and emerged galls, third instar parasitoid larvae and parasitoid pupae; Dade Co., Homestead, 3-13-89, leg. C. Campbell, 200 syconia, diameter 7–11 mm, 20 of these syconia with one to five *Ficiomyia* galls each. Midge larvae parasitized by *Physothorax bidentulus* Burks, pupae by an unidentified chalcidoid. Furthermore we reared species of *Pegoscapus* (Agaonidae), *Colyostichus, Idarnes* (Torymidae), and an eurytomid, probably a *Syceurytoma.* The latter form was also dissected from galls. Heavy mortality of wasps was caused by larvae of a staphylinid beetle and a few ant species; Dade Co., Miami, 3-15-89, leg. H. Nadel and J. C. Roskam, 200 syconia, diameter 5–8 mm, 30 galls, induced by *Ficiomyia,* larvae in second and third instar, parasitoids absent; Monroe Co., No Name Key, 8-7-88, leg. H. Nadel, 30 syconia, diameter 8 mm, with remnants of fig wasps and agaonid larvae, no galls; Monroe Co., No Name Key, 9-17-88, leg. H. Nadel, 17 syconia, diameter 8–10 mm, with fig wasp remnants, many galls with midge pupae and emerged adults; Monroe Co., Key Largo, 9-12-88, leg. H. Nadel, 22 syconia, diameter 4–5 mm, too young for ovipositing fig wasps; five syconia, each with one gall, one syconium with three galls, all with first instar midge larvae; Monroe Co., Key Largo, 3-28-89, leg. H. Nadel and J. C. Roskam, 30 syconia, galls absent, two kinds of ovaries containing agaonid and torymid wasps.

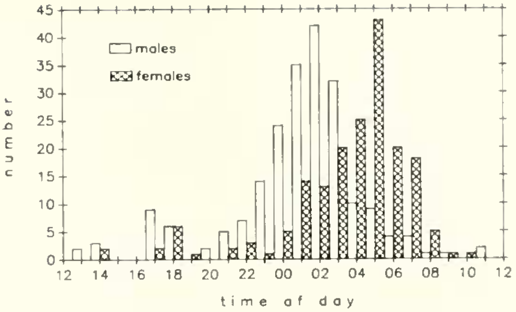


Fig. 24. Distribution of emergence of adult *F. perarticulata* from syconia of *Ficus citrifolia* in southern Florida. Data were combined from four days of hourly observation during April and May 1989.

ADULT EMERGENCE FROM GALLS

The formation of the crown-like ridge around the opening of the gall begins about two days before eclosion of *F. perarticulata.* The fig skin splits, exposing the whitish tissue of the syconial wall, and curls outward radially to form a crown around the exit area. The tissue within the base of the gall becomes moist and vicid. The pupa pushes its way head first to the gall exterior and comes to rest with about three-quarters of its length protruding from the fig surface. The adult ecloses after a few minutes, leaving the pupal skin partly embedded in the crown, and rests hanging from the side or bottom of the fig by its front and middle legs. The wings are fully expanded within five minutes and are capable of sustained flight within an hour after eclosion.

Daily emergence within a population is periodic, with a minor peak in late afternoon and a major peak during the night, and with males tending to emerge earlier than females during the major peak (Fig. 24). Within a single fig, emergence of all adults usually spans a few days, and may span even weeks, as suggested by our observations of second instar larvae in figs with already emerged galls.

Emergence occurs throughout the year in Florida, as *F. citrifolia* trees fruit asynchronously in relation to each other and thus afford year-round development by the gall midges. This scenario probably prevails over the entire range of the midge.

MATING

Mating probably occurs on or around the tree from which adults emerged. Females extrude their ovipositors directly after eclosion, apparently to emit pheromones. On three evenings around sunset we observed males, solitary and in small groups, flying in zigzag motion towards and around tips of branches. Males also frequently landed on fruits and leaves. We observed only one mating pair, which was on a fig at 17:45 on 6 December. The female, however, was captured by an ant either before or during copulation. The male continued to hang, head-down, by its terminalia for five minutes before disengaging from the female.

SEX RATIO

Both sexes may inhabit one fig. The sexual dimorphism in gall shape allowed us to determine midge sex ratio before mortality due to parasitism. In one sample of 13 fruits with 134 galls, 69 galls were male (sessile) and 65 were female (stalked), which is essentially a 1:1 ratio; however, in a sample of 50 fruits from a different location, 61 were male and 24 were female, which is highly male-biased (Chi-square = 16.11; $P < .005$). The sex ratio of emerged adults was studied in four other locations. Collection 1 yielded 32 adult males and 35 females; collection 2 yielded 32 males and 20 females; collection 3 yielded 70 males and 46 females; and collection 4 yielded 88 males and 81 females. The sex ratio in collection 3 deviated significantly from 1:1 (Chi-square = 4.97; $.025 < P < .050$). Apparently, sex ratio of *F. perarticulata* varies from equality to male-biased.

SYCONIAL GALL MIDGES IN OTHER GEOGRAPHIC AREAS

If close relatives of *Ficiomyia* exist, we would expect them in syconia of figs occurring elsewhere. Docters van Leeuwen-Reijvaan and Docters van Leeuwen (1926) listed 28 kinds of galls from Malaysian figs on leaves, stems, aerial roots, and three kinds in syconia. Samples of these fruit galls, dried and in alcohol, have been deposited in the Rijksherbarium at Leiden, the Netherlands. None of the syconia of this material bear galls of the type induced by *Ficiomyia.* We dissected one mature larva from a syconium. This larva differs in many respects from *Ficiomyia* larva and probably belongs to the tribe Cecidomyiini. Barnes, in Williams (1928), described two species, one cecidomyiine and the other an asphondyliine, from fruits of figs native to the Philippines. These species, together with a cecidomyiine occurring in India, have also been listed in Barnes (1948). Although seven species of figs occur in Japan (Ohwi 1965), no cecidomyiids have been reported from them (Yukawa 1971). Finally, Mani (1973) distinguished eight kinds of leaf galls, but none is induced by Oligotrophini.

Two females, undoubtedly belonging to *Ficiomyia,* have been collected in a light trap in Dominica (West Indies, Clarke Hall, 1–10 February and 1–10 March 1965, leg. W. W. Wirth). The sole complete flagellum yields a count of only 33 flagellomeres and the hypoproct is slightly longer (41 μm) in one specimen. All remaining measurements are within the ranges given for *F. perarticu-*

lata. Because of the low number of flagellomeres this material might belong to a new species. More material and host data are required, though, to draw a conclusion and to provide a formal description.

Possible *Ficiomyia* parasitoids, in the genus *Physothorax,* have been described from Brazil, reared from big, stalked galls in the syconia of *F. doliaria* Mart. (Mayr 1885, 1906, Müller 1886). We cannot conclude, however, whether this indicates the presence of *Ficiomyia* in Brazil, since *P. russelli* Crawford and *P. pallidus* Ashmead also emerge from large, stalked galls in *F. aurea.* These galls are not induced by *Ficiomyia,* but probably by torymid sp. The genus *Physothorax* is not known outside the New World (Bouček et al. 1981). Hence, although our data are incomplete, there is no evidence that *Ficiomyia* or its parasitoid, *Physothorax,* occurs outside the New World. *Syceurytoma* has been described from African material (Bouček et al. 1981), but again there is no evidence that any of its species are associated with *Ficiomyia.*

ACKNOWLEDGMENTS

We thank M. Zandee, Institute of Theoretical Biology, University of Leiden for his statistical help. E. Grissell, Systematic Entomology Laboratory checked the identifications of the parasitoids. H. Heyn is gratefully acknowledged for drawing some of the figures. For his critical and helpful reviews of this manuscript and for the loan of specimens in his care we thank R. J. Gagné, Systematic Entomology Laboratory, Washington, D.C.

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